Early Journal Content on JSTOR, Free to Anyone in the World

This article is one of nearly 500,000 scholarly works digitized and made freely available to everyone in the world by JSTOR.

Known as the Early Journal Content, this set of works include research articles, news, letters, and other writings published in more than 200 of the oldest leading academic journals. The works date from the mid-seventeenth to the early twentieth centuries.

We encourage people to read and share the Early Journal Content openly and to tell others that this resource exists. People may post this content online or redistribute in any way for non-commercial purposes.

Read more about Early Journal Content at http://about.jstor.org/participate-jstor/individuals/early-journal-content.

JSTOR is a digital library of academic journals, books, and primary source objects. JSTOR helps people discover, use, and build upon a wide range of content through a powerful research and teaching platform, and preserves this content for future generations. JSTOR is part of ITHAKA, a not-for-profit organization that also includes Ithaka S+R and Portico. For more information about JSTOR, please contact support@jstor.org.

THE STRUCTURE OF THE STARCH GRAIN.[1]

HENRY KRAEMER.

(WITH PLATE XI AND TEXT FIGURES)

THERE have been a number of hypotheses advanced to explain the origin, nature, and structure of the starch grain. (1) It was originally considered to be a bubble filled with a liquid, or, as stated by Nägeli, "einer mit Flussigkeit gefüllten Blase." According to Von Mohl, Raspail considered that the starch grain consists "aus einer in Wasser unlöslichen blasenformigen Hülle und einem löslichen gummiartigen Inhalte." (2) Then (1834) it was considered that to a central or excentral point layer after layer was added, the peripheral layers thus being the last formed, this view having been advanced by Fritsche (**1**) and supported in a more or less modified form by Treviranus (**2**), Lindley (**3**), Schleiden (**4**), Braun (**5**), Schacht (**6**), Crüger (**7**), and Unger (**8**). (3) Payen (**9**) in 1838 conceived the idea that growth took place from the outside, that through one or more funnel-like openings at the periphery of the grain new substances entered and new layers were formed therefrom, the outer layers thus being the oldest, in contradistinction to the view advanced by Fritsche. (4) Then followed a series of contributions in which the growth of the starch grain was likened to that of the cell wall and the formation of cells. This theory, with certain modifications, was advocated by Münter (**10**), Walpers (**11**), Reissek (**12**), C. Nägeli (**13**), Kützing (**14**), and Hartig (**15**). (5) While Nägeli (**16**) recognized that assimilation starch arose in plastids, he considered that most starch grains arose free in the cell sap under the influence of living protoplasm, and it was not until 1880 that Schimper (**17**) demonstrated that all starch grains develop within plastids and that in the reserve starch grains the leucoplastids finally disappear. Schimper further showed that the outer portion of the grain is the youngest, and thus substantiated the view of Fritsche concerning its development.

---

[1] An abstract of a preliminary paper on this subject was presented to the Society for Plant Morphology and Physiology, December 1899.

If we consult any of the standard works on organic chemistry, we find that the formula which is generally accepted for starch is $n\ (C_6\ H_{10}\ O_5)$, this being the formula recognized by Pfeffer, Tollens, and Mylius. It is supposed that the molecular composition is quite complex, the grain being composed of different single groups of $C_6\ H_{10}\ O_5$ or multiples of the same. While this formula may be accepted in a general way, still it has been shown that there are at least two substances which enter into the composition of the starch grain. Nägeli (**16**) has shown that the starch grain consists of two different substances, one which is soluble in ferments, and called by him granulose, and another which is insoluble in saliva, and called by him starch cellulose. He showed that when the starch grain was deprived of its water the lamellae were not apparent, and therefore he concluded that the layering was due to a difference in the amount of water present in the different lamellae. This view has given rise to the formula suggested by W. Nägeli (**18**) for the starch grain, which is $6C_6\ H_{10}\ O_5 + H_2\ O$, or $C_{36}\ H_{62}\ O_{31}$. Maschke (**25**) considered that the starch grain consisted of alternate layers of cellulose between which starch substance was deposited in two modifications, one soluble in water forming the light-colored lamellae, and another insoluble in water forming the dark layers. This view was not adopted, however, and Nägeli's theory prevailed until 1886, when Arthur Meyer (**19**) demonstrated that the substance termed cellulose by Nägeli, and which was termed "farinose" by Von Mohl (**20**), gave reactions similar to artificially prepared crystals of amylodextrin. In 1895 Meyer (**21**) further considered the composition of the starch grain and stated that it is made up of (1) α–amylose, (2) β–amylose, and (3) amylodextrin, a decomposition product of amylose. He also expressed the opinion that inasmuch as there is an anhydride of dextrose which does not readily take up water, there is probably also an anhydride of amylose which even on boiling with water is hydrated with difficulty, and that this is the substance that has given rise to the belief that there is present a starch cellulose. This latter term, according to Meyer, has been used for a number of different substances: (1) mixtures of amylodextrin and α–amylose; (2) solutions of α–amylose and β–amylose; (3) solutions of β–amylose with various other substances, as nitrogen-holding substances, impure fatty products, pure amylodextrin, and the walls of plant cells which are contained in commercial starches unless carefully purified. He obtained the α–amylose upon treating starch paste (Stärkekleister) with malt solutions (Malzauszug) and by the action of hot dilute solutions of hydrochloric acid upon the whole starch grain. The portion remaining (β–amylose) is distinguished from the portion dissolved in that it is not soluble in water and becomes slightly reddish, and not blue with iodine.

One of the earliest views in regard to the development of the starch grain was that new layers were added to those previously formed, these being separated from each other by layers of air which were later called "Adhäsionsflächen," "Contactflächen," and "Grenzflächen" by Dippel (**22**), Strasburger (**23**), and Krabbe (**24**) respectively. These terms, however, have been mostly used by these authors in describing the structure of cell walls. In 1858 Nägeli (**16**) advanced the theory that the starch grain consists of elementary particles, later termed by him "micellae," which he supposed to have the form of parallelopipedal prisms with rectangular or rhomboid bases. Furthermore, according to Nägeli, these micellae possess a watery film, are embedded in a mother liquor which differs from them in composition, and are held together by certain forces. The growth of the starch grain is effected by the interpolation of new material among the particles already formed, this new substance being utilized in part in increasing the size of the micellae already formed, and also to form new micellae, which develop and arrange themselves according to the laws which the micellae previously formed have obeyed This theory is known as the "intersusception theory," while the earlier one is spoken of as the "apposition theory." In addition to these two views in regard to the structure of the starch grain, Schimper (**17**) considered that it is made up of sphere-crystals which he called

"Spharokrystalloide." Meyer (**21**) has enlarged upon this view and considers the starch grain to be made up of two kinds of acicular crystals, which he calls "Trichiten," these being composed of α–amylose and β–amylose, there being also present in the grains that are colored red with iodine, amylodextrin and dextrin. He further says that most starch grains consist altogether or nearly so of amylose, and that these are colored blue with iodine. These latter starch grains are made up of sphere-crystals of amylose, arranged in layers, and these layers may consist of crystals of either α–amylose or β–amylose, or both, some starch grains containing in addition, as already stated, large amounts of amylodextrin and dextrin.

Starch grains are distinguished from one another by the following particulars: (1) The origin in the plant; (2) the shape of the grain; (3) the size of the grain; (4) the position of the point of origin of growth;[2] (5) the shape of the point of origin of growth; (6) distinctness of lamellae; (7) the direction of the lamellae; (8) behavior toward dilute iodine solutions; (9) the temperature at which the "Kleister" or paste is formed and its consistency; (10) the behavior toward various reagents, as chromic acid, calcium nitrate, chlor-zinc-iodide, sulphuric acid, diastase, etc.; (11) the appearance as viewed by polarized light. These differences in starch grains not only from different sources, but even in those of the same origin, tend to show that instead of starch being a uniform substance, it is made up of several substances, these occurring in varying proportions but appearing to be more or less definitely arranged.

The author may briefly state that he conceives the reserve starch grain to be the direct product of the polymerization of soluble carbohydrates of either the glucose or cane sugar group, together with the abstraction of water. This process is carried on under the influence of an organized body — either protoplasm, or a plastid, or both. The products thus formed consist of two

[2] The terms "hilum" and "nucleus" have been employed to distinguish the central or excentral marking, around which the lamellae or layers of the grain are arranged. These terms, however, are open to criticism, inasmuch as they are employed for another and specific purpose. The expression "point of origin of growth" seems to be better on account of its being less confusing, and is moreover descriptive and accurate.

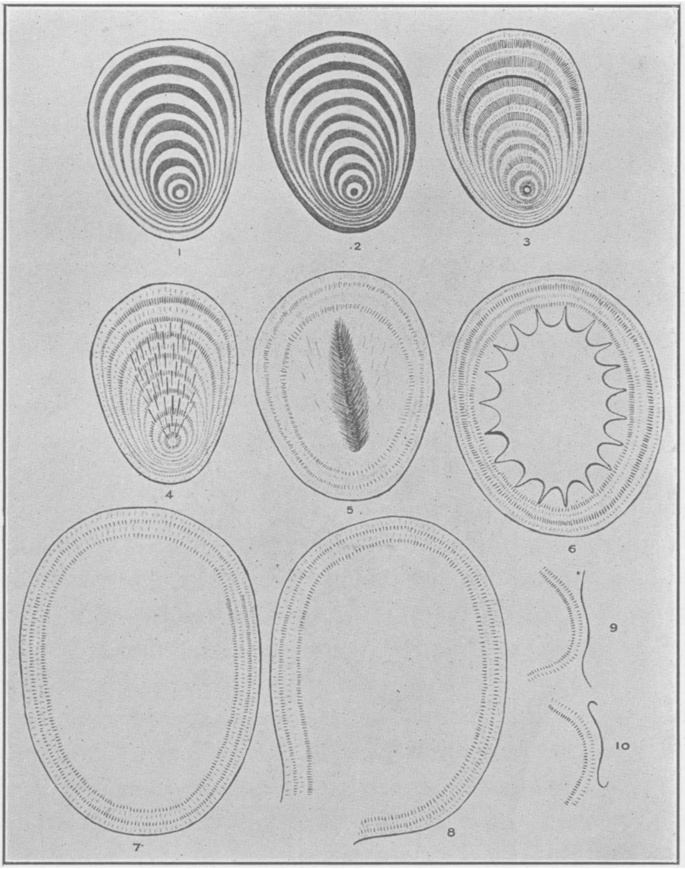
crystalloidal substances, namely starch cellulose[3] and granulose, and also a colloidal substance. These occur as follows: (*a*) In the point of origin of growth we find the colloidal substance associated with a small proportion of cellulose as also in the alternate lamellae; (*b*) in the other layers occurs the granulose associated with a small amount of colloidal substance and possibly also some cellulose; (*c*) the peripheral layer of the grain is not readily acted upon by reagents and is quite elastic and more or less porous, probably consisting of an anhydride of cellulose; (*d*) in some cases some of the dextrins or some of the non-colloidal or crystalline carbohydrates, as maltose, dextrose, levulose, etc., may be present, but these are probably formed as a result of alterations taking place in the grain.

There have been a number of important contributions on the subject of the origin and structure of the starch grain, and while the views of the authors appear to be more or less at variance, still this is not to be wondered at, and it is highly probable that future observations will harmonize some of these conflicting views.

The illustrations of potato starch grains in the different text-books show two kinds of grains, one in which the point of the origin of growth and alternate lamellae are light in color, as figured by Sachs (**26**); and the other in which the corresponding parts are dark in color, as figured by Strasburger (**27**). There is in reality no difference in these grains, this apparent difference being due to the manner of focusing upon them (*figs. 1, 2*), that is, whether viewing the lamellae from above or from below, or, as the Germans would say, by "tiefe oder höhe Einstellung." The two views of the successive lamellae thus obtained may be compared to the appearances obtained with two entirely different substances, the one corresponding to a more or less definite solid substance, as an oil globule, and the other to a body such as an air bubble (or vesicle filled with air or any other gaseous or rarefied material). The appearance as observed in the oil globule corresponds to that of the layer next to the point of origin of growth and the layers alternating with it. The appearance of

---

[3] Cellulose was a term first applied by Nägeli (**16**) and corresponds to the farninose of Von Mohl (**20**) and probably to the β-amylose of Arthur Meyer (**21**). Granulose another term which is generally accepted to have been coined by Nägeli (**16**), was adopted by Von Mohl (**20**) and apparently corresponds to the α-amylose of Arthur, Meyer (**21**).



FIGS. 1–10.—Potato starch grains, showing the effect of chromic acid and other reagents.

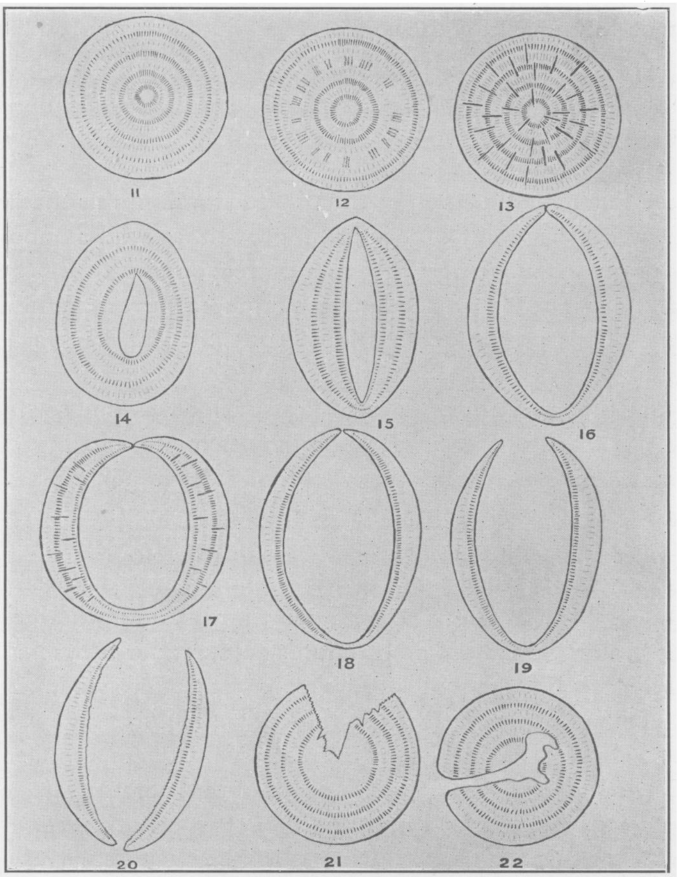
the air bubble corresponds to that of the point of origin of growth and the layers alternating with it. There is this difference, however, that instead of the purplish hue so characteristic of the air bubble, there is a reddish field in the starch grain which may be taken as indicating that it is of an entirely different composition. A possible explanation of this phenomenon may be that in the air bubble the violet rays, owing to their length and velocity, completely overshadow the red rays; whereas in the starch grain the layers containing other substances offer a resistance to and refract the violet rays and leave the red only in view. As a result of this physical examination of the grain we observe that the successive layers differ in density, and that these correspond to the "water-poor" and "water-rich" lamellae described by Nägeli (**16**).

We further find in some of the potato starch grains that at the periphery of the point of origin of growth, as well as upon the inside of one or more of the layers corresponding to it, there is a dark line much resembling the peripheral layer of the grain (*fig. 3*). This probably led Dippel (**22**), Strasburger (**23**), and Krabbe (**24**), to consider that the lamellae did not differ in character, but that this appearance of lamellation was due to lines of contact, as already stated. Krabbe in the chapter dealing on the "Spiralstreifung der Bastfastern" further distinguishes between "Grenzflächen" and "Contactflächen." He says: "Schichten mit derselben Streifung, jedoch mit verschiedener Steilheit derselben, vorliegen, da wird ihre gegenseitige Abgrenzung dadurch noch deutlicher, das die Grenzflächen der Spiralbänder in der Contactfläche der Schichten nicht immer aufeinander Stossen."

A further evidence that there is a marked difference in the layers of the grain is the effect produced by staining reagents (*figs. 29, 30*). On treating starch grains with weak aqueous solutions of safranin and gentian-violet,[4] it is observed that certain parts of the grain take up these stains more readily than others. The gentian violet stain is more pronounced in its effect upon the potato starch grain (*fig. 35*), it being held by the point of origin of growth and the lamellae alternating with it. Safranin, on the other hand, is a better differential stain for wheat starch grains (*figs. 36, 39*), being held in certain of the lamellae (usually not more than three or four of them being affected) and in numerous radial clefts or channels. Corn starch (*fig. 40*) does not appear to take up these stains as readily as either wheat starch or potato starch, and there is no differentiation of the lamellae.

---

[4] The method used by the author consisted simply in treating the freshly isolated starch grains, or the commercial starches, with weak aniline dye solutions and allowing them to dry at an ordinary room temperature.



FIGS. 11–22.—Wheat starch grains; *11–20*, showing the effect of chromic acid and other swelling reagents; *21–22*, showing a direct disintegration of the grains through the action of ferments.

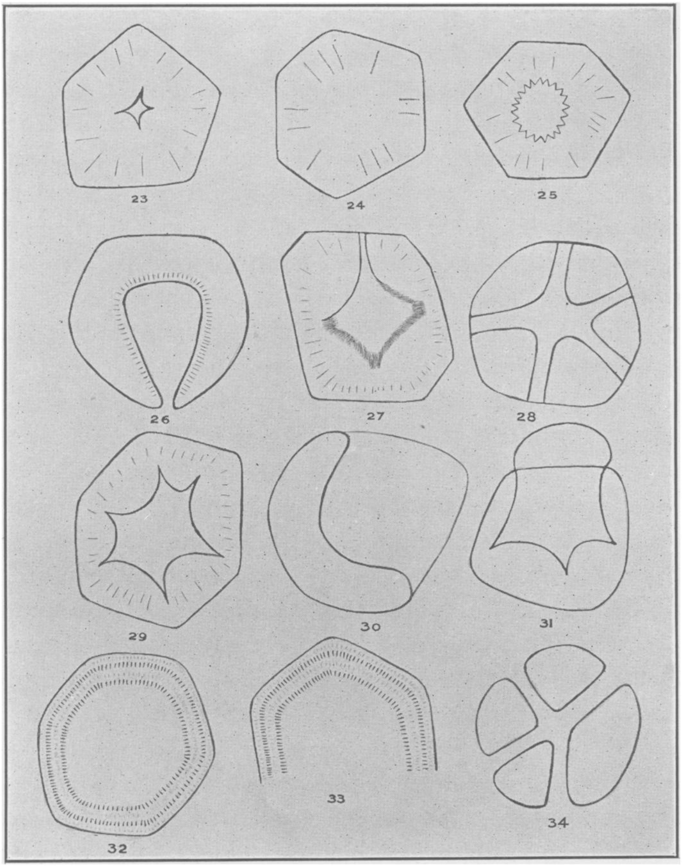
This is probably due to the peripheral layers being denser and less permeable. Salter (28) in speaking of the staining of the grain says that it is dependent upon the absorption of the aniline dye, and that in no case does it seem to have a selective or specific action on the layers. The figures of Salter, however, show that the stain is taken up by certain parts of the grain more than others, and in another place he states that "die Lamellen die im frischen Stärkekorn als dunklere Linien erscheinen sind diejenigen welche den Farbstoff am reichlisten einsaugen." In speaking of Meyer's work he goes on to say: "Meyer erwahnt dass bei der Farbung mit Methylviolet der Farbstoff besonders von den weicheren Lamellen beibehalten wird." The only unfortunate thing is that we do not know to what layers these authors refer when they speak of "weicheren Lamellen" and lamellae with "dunklere Linien." There seems to be no doubt, however, that what they have in mind corresponds to my own observations, that is, it is the layers which are colloidal in character which take up the stains; in other words, the point of origin of growth and the layers alternating with it.

Another interesting feature serving to differentiate the layers of the starch grain is the behavior toward dilute iodine solutions. The layers which are not affected by the aniline stains become blue with iodine, the alternate layers and the point of origin of growth remaining unaffected. The layers thus affected by iodine are the ones which are rich in granulose and are more clearly defined in the grains of potato and wheat starch than in corn starch. These layers become crystalloidal in character on treatment with water at 60° or 65° C. for about an hour, and also with chromic acid, calcium nitrate, saliva, and other reagents.[5]

The behavior of potato starch toward these reagents may be briefly summarized as follows (*figs. 1–10*): The first effect of the reagent is to make the lamellae more distinct (*figs. 1–2*); this is followed by the development of the crystalloidal character of the lamellae (*fig. 3*), which is most pronounced in those colored blue with iodine; this is followed by the production of small tracts or channels (*fig. 4*) connecting the contiguous lamellae, particularly in the middle of the grain; succeeding this there is the formation of channels which are larger and plume-like in appearance (*fig. 5*), the grain meanwhile swelling quite perceptibly, the middle portion becoming clearer and assuming a zigzag outline (*fig. 6*), between which and the periphery of the grain a number of crystalloidal lamellae arise (*fig. 7*); the grain now becomes spherical and marked by a number of concentric lamellae near the periphery; the latter finally ruptures (*fig. 8*) and then follows a gradual solution of the grain, the peripherical layer sometimes recurving like the cutin layer of an epidermal cell on treatment with sulphuric acid (*figs. 9, 10*).

---

[5] Proc. Acad. Nat. Sci. Philadelphia **53**: 450. 1901.



FIGS. 23–34.—Corn starch grains, showing the effect of chromic acid and other swelling reagents.

In wheat starch (*figs. 11–22*) the development of the crystalloidal character of the lamellae (*figs. 11, 12*) is followed by the formation of narrow, interrupted or continuous, radial channels near the periphery of the grain (*fig. 13*), which are sometimes connected with lamellae occurring near the middle of the grain; the grain meanwhile swells quite perceptibly, the center becomes clearer (*fig. 14*), the contents are crowded into crescent-shaped halves which are still slightly connected at the poles (*figs. 15–17*); the contents of each of the halves of the grain consist of crystalloidal lamellae in which are then produced small tracts or channels connecting the contiguous lamellae (*fig. 17*); the halves in some instances finally separating and slowly dissolving (*figs. 18–20*). In some cases, on the other hand, there is a corrosion of the grain at the periphery, followed by gradual disintegration without the separation into halves (*figs. 21, 22*).

The first effect of reagents upon the corn starch grain (*figs. 23–34*) is to bring out the point of origin of growth (*fig. 23*), the latter becomes larger and in some cases more or less zigzag (*fig. 25*) in outline; between this and the periphery of the grain arise more or less interrupted or continuous radial channels (usually the latter); the crystalloidal structure of this grain develops slowly and is most pronounced when the grain has swollen to two or three times its normal size; at this stage we find that the center of the grain has become clear and the point of origin of growth has become obliterated in some cases (*fig. 24*), and between it and the periphery occur numerous crystalloidial lamellae similar to those observed in the potato starch; finally the peripheral layer ruptures and there is a gradual disintegration of the grain (*figs. 26, 30, 33*). Sometimes the grain appears to separate into as many parts as there were arms to the point of origin of growth (*figs. 27, 28, 34*), particularly when acted upon by saliva or diastase.

A number of authors since the time of Nägeli have shown that the lamellae of starch grains differ in constitution and structure, and that there are at least two distinct kinds of lamellae. This view is confirmed not only by a microphysical examination of the grain, and by treatment with weak solutions of iodine and aniline stains, but also by treatment with water and various reagents as just pointed out. Both Salter and Meyer appear to hold to the theory that there is a distribution of crystalloidal substance in particular lamellae. Salter quotes Meyer as saying: "die schattierten Schichten bedeuten die schwach lichtbrechenden relativ lockeren, an fester Substanz relativ armen, an Interstitien reichen Schichten, die hellen sind also die stark lichtbrechenden Schichten aufzufassen, welche die meiste feste Substanz enhalten." Here again it is unfortunate that the descriptions do not enable us to determine which layers are meant. It is likely, however, that the layers described as "schattirten Schichten" are the colloidal layers, and those designated as "hellen Schichten" are the crystalloidal layers.

In summing up the observations herewith presented, we find that the starch grain consists of colloidal and crystalloidal substances, these being arranged for the most part in distinct and separate lamellae, that is, at the point of origin of growth, and in the alternate lamellae the colloidal substance preponderates, associated with the crystalloid cellulose; whereas in the other layers the crystalloidal substance, consisting for the most part of granulose, occurs in greater proportion.

As a further evidence of the presence of these crystalloidal and colloidal areas we may say that the peculiar behavior of the colloidal layers toward aniline stains is analogous to the behavior of a section containing mucilage cells toward these dyes, the latter being taken up by the mucilage cells alone. Furthermore, as the characteristics of mucilage cells are most pronounced in anhydrous media, as concentrated glycerin, so a similar effect is observed in the starch grain, but owing to the action of the glycerin in readily forming soluble starch, the preparations of the starch grain, like that of the cell wall, when thus stained are best preserved in Canada balsam.

The crystalloidal character of certain of the lamellae as observed in connection with the swelling of the grain might be considered to be in the nature of microscopic clefts, but it should be said that we know of no colloid that behaves in this manner, and such an assumption does not seem to be well founded. Furthermore, this appearance (crystalloidal) might be considered as due to an internal folding of the substance of the lamellae, but this would only arise in case of a contraction or reduction in the area of the lamellae ; but as we have already seen the grain is swollen from two to four times its original size, and even in the fragments of the disintegrating grains the crystalloidal character is pronounced. It seems more likely, as I have already pointed out, that the reason this structure is not apparent under natural conditions is because the refractive properties of the crystalloidal substance so nearly resembles that of the associated colloid. The use of certain reagents, however, which are more or less penetrating in their action, cause an imbibition of water by the colloidal portions with consequent swelling of the grain, and hence a contrast in refractive power with the more insoluble crystalloidal substances.

COLLEGE OF PHARMACY,
Philadelphia.

LITERATURE CITED.

1. FRITSCHE : Poggendorff's Annalen der Physik und Chemie **32** : 1834.
2. TREVIRANUS : Phys. der Gewächse **2**:23.
3. LINDLEY : Introduction to Botany, Ed. 3, p. 44.
4. SCHLEIDEN : Grundzüge **3**^{1} : 187.
5. BRAUN : Verjüngung, p. 212.
6. SCHACHT : Lehrbuch der Anat. und Phys. der Gewächse **1** : 58.
7. CRÜGER : Bot. Zeit. **10**:41. 1854.
8. UNGER : Anat. und Phys. der Pflanzen, p. 115.
9. PAYEN: Ann. Sci. Nat. **10**:5, 65, 161. 1838.
10. MÜNTER : Bot. Zeit. **3**:197. 1845.
11. WALPERS : Bot. Zeit. **9**: 339. 1851.
12. REISSEK : Flora **5**:13. 1847.
13. NÄGELI, C.: Zeitschrift für wissenschaftliche Botanik von Schleiden und Nägeli 117. 1847.
14. KÜTZING : Grundzüge der Philos. Bot. **1** : 263.
15. HARTIG, Th.: Bot. Zeit. **13**:905. 1855 ; **14**:350. 1856.
16. NÄGELI, C.: Die Stärkekörner. Pflanzenphysiologische Untersuchungen. Zurich. 1858.
17. SCHIMPER : Bot. Zeit **38**:881. 1880 ; **39**:185, 201, 217. 1881.
18. NÄGELI, W.: Beiträge zur naheren Kenntniss der Starkegruppe. Munich. 1874.
19. MEYER, A.: Bot. Zeit. **39**:841–857. 1881 ; **44**:697, 713. 1886.

20. VON MOHL: Bot Zeit. **17**:226. 1859.

21. MEYER, A.: Untersuchungen über die Stärkekörner. Jena. 1895.

22. DIPPEL: Bot. Zeit. **9**:409. 1851: Abhandl. Senkenb. Gesell. **10**:181.

23. STRASBURGER: Ueber den Bau und das Wachsthum der Zellhäute. Jena. 1882, p. 64; Ueber des Wachsthum vegetabilscher Zellhäute. 1889, p. 147.

24. KRABBE: Jahrb. Wiss. Bot. **18**:346. 1887.

25. MASCHKE: Jour. Prakt. Chem. **56**:400. 1852.

26. SACHS: Lehrbuch der Botanik. Leipzig. 1874.

27. STRASBURGER: Das botanische Praktikum. 1884 and 1887.

28. SALTER: Jahrb. Wiss. Bot. **32**:117. 1898.

29. ROTHERT: Ber. Deutsch. Bot. Gesell. **15**:231.

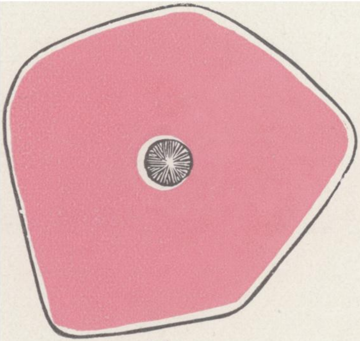
30. FISCHER: Ueber Inulin, etc. Cohn's Beiträge zur Biologie der Pflanzen **8**:53. 1898.

EXPLANATION OF PLATE XI.

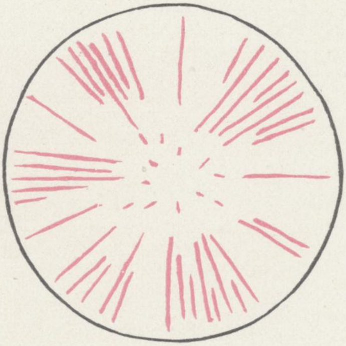
FIG. 35. Potato starch grain treated with weak aqueous solution of gentian-violet.

FIGS. 36–39. Wheat starch grains treated with weak aqueous solution of safranin.

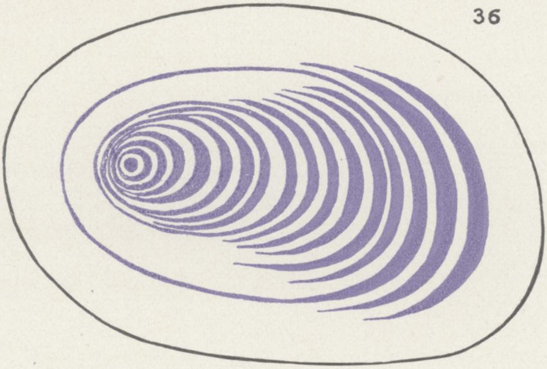
FIG. 40. Corn starch grain treated with weak aqueous solution of safranin.



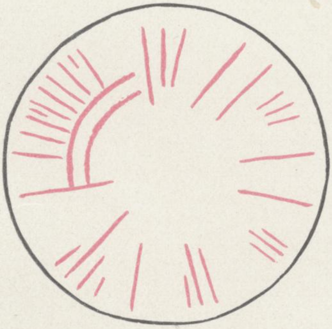
35



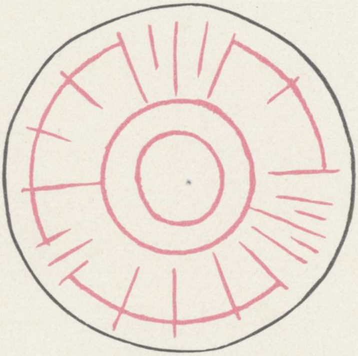
36



37



38



39

KRAEMER on THE STARCH GRAIN